

# Compound Eye Fine Structure in *Paralomis multispina* Benedict, an Anomuran Half-Crab From 1200 m Depth (Crustacea; Decapoda; Anomura)

EISUKE EGUCHI<sup>1</sup>, MARI DEZAWA<sup>2</sup>, AND V. BENNO MEYER-ROCHOW<sup>3</sup>

<sup>1</sup>Department of Biology, Yokohama City University, 22-2 Seto, Kanazawa-ku, Yokohama 236, Japan, from Japan Marine Science and Technology Center (JAMSTEC), Natsushima-cho, Yokosuka, 237, Japan; <sup>2</sup>Department of Anatomy, School of Medicine, Chiba University, Inohana, Chuo-ku, Chiba 260, Japan; and <sup>3</sup>Department of Biology (Section Animal Physiology), University of Oulu, SF-90570 Oulu, Finland

**Abstract.** Fully grown, unsexed specimens of the anomuran half-crab *Paralomis multispina* Benedict were obtained from a depth of 1200 m, and the eyes of three individuals were prepared for light and electron microscopy. In their outer appearance the compound eyes of *Paralomis* resemble those of common shallow-water half-crabs (e.g., *Petrolisthes*), but facets in *Paralomis* were about 3 times larger in diameter (i.e., 60  $\mu\text{m}$ ) and at least twice as long. Interommatidial angles ranged from 3° to 5°. The proximal width of the crystalline cone in *Paralomis* was 10 times that of its equivalent in the *Petrolisthes* eye, and the rhabdom—although only twice as long—had a radius that was 7 times greater distally and 4 times greater proximally. A clear-zone between cones and rhabdom was not developed, and cross sections of crystalline cones revealed rounded rather than square profiles. A distal retinula cell (R8) was absent, and all regular retinula cells (R1–R7) protruded microvilli of about 0.11  $\mu\text{m}$  diameter in many (and not only two) directions. A maximum rhabdom occupation ratio of 85% was found in the *Paralomis* retinula, whereas in the shallow-water half-crabs the comparable figure was 35%. *Paralomis* featured a wide, rhabdomless space between basement membrane and proximal rhabdom ends; the space was occupied by reflecting cells. Primary screening pigment cells and their dark granules were present; secondary screening pigment cells, however, were replaced

by reflecting cells. The anatomical modifications in the *Paralomis* eye are consistent with habitat-related adaptations seen in the eyes of other benthic and slow-moving deep-water crustaceans, but not with those of euphausiids. We conclude that the eye of *Paralomis* functions as an apposition eye, designed to maximize photon capture, especially from point sources (i.e., bioluminescence) rather than extended sources. We estimate that the *Paralomis* eye is at least 150 times more sensitive to light than the eye of shallow-water *Petrolisthes*.

## Introduction

Animals that live in or colonize greater oceanic depths face three major physical challenges (Marshall, 1957; Thorson, 1972): (a) atmospheric pressure increases by 1 with every 10 m of water; (b) ambient light levels become progressively reduced, and the spectral composition of the downwelling light changes as depth increases; and (c) the temperature of the water falls as the distance to the surface increases, except in the polar oceans (where bottom temperatures may actually lie a few degrees above those of the surface) and near hydrothermal vents.

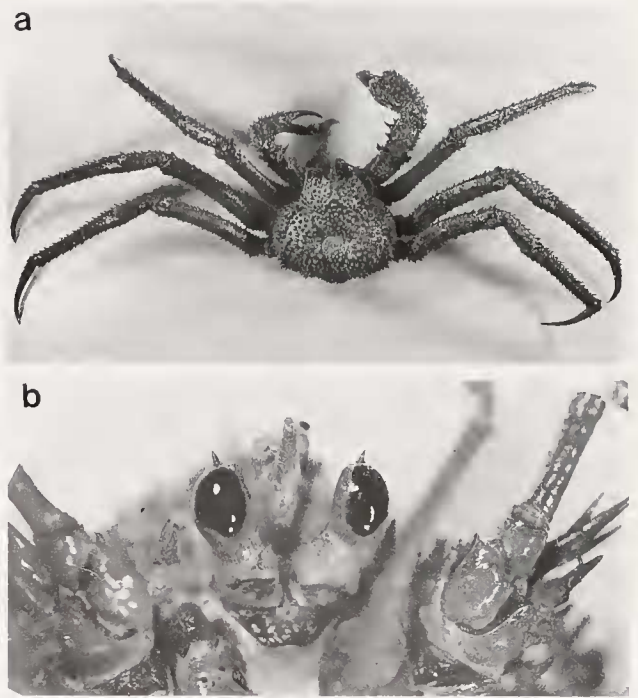
The eyes of animals are usually attuned to the photic conditions under which they operate (Forward *et al.*, 1988), but environmental temperature and pressure also influence certain structural and functional parameters of photoreception through their effects on membrane fatty acid content and composition (Cossins and Macdonald, 1989; Sebert *et al.*, 1992; Kashiwagi *et al.*, 1996). Based

on a number of light microscopical (Beddard, 1890; Welsh and Chace, 1937, 1938; Zharkova, 1970, 1975; Bursey, 1975) and electron microscopical studies of deep-water crustacean eyes (Elofsson and Hallberg, 1977; Ball, 1977; Hallberg, 1977; Meyer-Rochow and Walsh, 1977, 1978; Hallberg *et al.*, 1980; Gaten *et al.*, 1992; Gaten, 1994; Nuckley *et al.*, 1996), certain general trends concerning their anatomy and performance in relation to depth have become apparent.

Bath pelagic and benthic species of depths exceeding 1000 m usually exhibit small and degenerate eyes (similar to those of species known from marine caves (Meyer-Rochow and Juberthie-Jupeau, 1987). Crustaceans inhabiting zones above 1000 m, on the other hand, frequently possess adaptations such as enlarged ommatidia, more voluminous rhabdoms, presence of retinal reflectors, *etc.*, to improve the efficiency of photon capture. Often such adaptations enhance overall sensitivity at the expense of acuity, but in cases where acuity apparently suffers little degradation, regional eye modifications and special optical designs may be employed as, for instance, in the Euphausiidae (Land *et al.*, 1979; Hiller-Adams and Case, 1984). Most euphausiids, however, are luminescent and thus not necessarily representative of other groups of crustaceans. For that reason and the fact that few species of deep-sea crustaceans have had their photoreceptors studied, we decided to examine the eyes of the anomuran decapod half-crab *Paralomis multispina* from a depth of 1200 m and compare them with those of shallow-water anomurans investigated earlier (Eguchi *et al.*, 1982; Meyer-Rochow *et al.*, 1990; Gaten, 1994).

### Materials and Methods

Several unsexed specimens of *Paralomis multispina* Benedict (Decapoda, Anomura, Galatheoidea) with carapace widths ranging from 5 to 11 cm and maximum body lengths (from head to tail) of 11.5 cm (Fig. 1a) were obtained in March 1992. Collections were made from the "Hatsushima seep" (Ohta *et al.*, 1987) at a depth of 1200 m about 5 km off Hatsushima Island in Sagami Bay (Shizuoka Prefecture, Japan) during a cruise of the manned research submersible *Shinkai 2000* (JAMSTEC). The half-crabs themselves are not considered to be thermophilic, although they occurred in association with the giant clam *Calymptogena soyae*, vestimentiferan tube worms, gastropods, and polychaetes (Hashimoto *et al.*, 1987) in an area that was characterized by an extremely high methane content. The half-crabs were picked up from the seafloor with remotely controlled artificial arms and put in a basket attached to the outside of the submersible. It took about 1 h for the submersible, with the collected animals, to reach the surface at about 1700 h.



**Figure 1.** Photographs of *Paralomis multispina*. (a) Dorsal view of specimen with carapace width of 11 cm and legs 30 cm long. (b) Close-up of head region with pair of eyestalks and black shiny eyes, each measuring about 4 mm in length in this specimen.

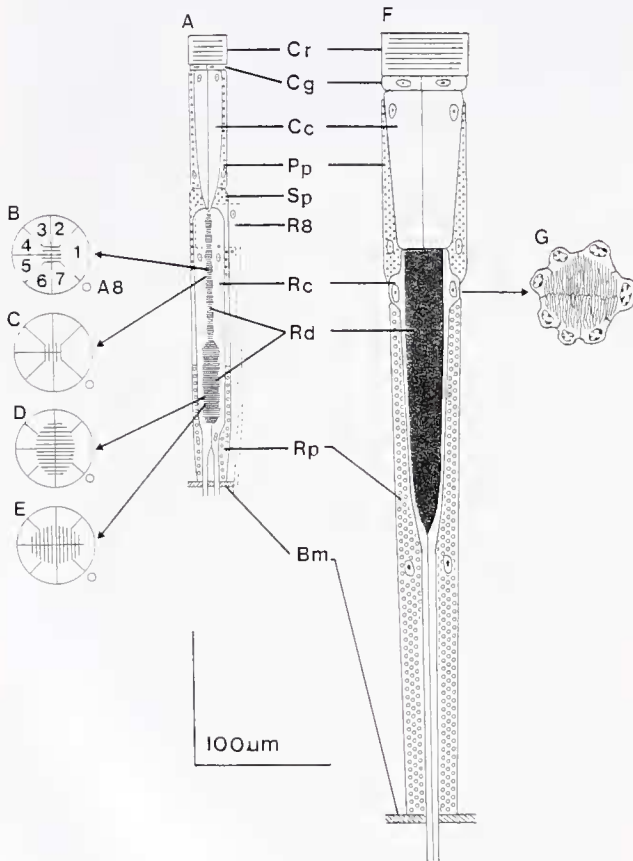
During capture, the animals were exposed to 10,000–20,000 lux bright sunlight for about 20 min, but immediately after they had been hauled on board the mothership *Natsushima*, the compound eyes of three individuals were fixed for 12 h at 4°C in 2% glutaraldehyde and 2% paraformaldehyde solution, buffered to a pH of 7.3 with 0.1 M cacodylate buffer. The dissections were carried out under dim red light to minimize further exposure to light and structural damage (*cf.* Meyer-Rochow, 1994). After a brief wash in buffer, the specimens were postfixed for 2 h in 2% OsO<sub>4</sub> solution, using the same buffer as before, and dehydrated in a graded series of acetone before being embedded in Epon 812. Ultrathin sections, cut with a diamond knife, were picked up on uncoated 200-mesh copper grids and stained with uranyl acetate and lead citrate for a few minutes. Observations were carried out under a JEM 1200EX transmission electron microscope, operated at 80 kV.

### Results

In their external appearance the compound eyes of the deep-sea anomuran *Paralomis multispina* (Fig. 1b) resemble those of other common anomuran shore-crabs (*e.g.*, genus *Petrolisthes*; Eguchi *et al.*, 1982; Meyer-Ro-

chow *et al.*, 1990), but overall the eyes are considerably larger. They are oval in outline and measure  $3.5 \times 2.5$  mm in an individual of about 10 cm carapace width. Each eye sits at the tip of an eyestalk that is 4–5 mm thick and 12 mm long; thus inter-eye distances and the precise location of the eyes in space are to a certain extent variable. Ommatidial numbers increase with age; whereas a specimen with a carapace length of 5 cm has about 1500 facets, some 2400 were counted in a specimen with a carapace width of 10 cm.

Interommatidial angles apparently do not change significantly with age and measure about  $3^\circ$ – $5^\circ$ . Figure 2 provides a comparison between the ommatidia, shown in identical scale, of a shallow-water anomuran and the deep-water species *Paralomis multispina*. Biometrical



**Figure 2.** Diagrammatic comparison of comparable ommatidia of *Petrolisthes* sp. (A–E), found in shallow water, and *Paralomis multispina* (F, G), found in the deep-sea at the same relative scale. A8 = axon of distal retinula cell R8; Bm = basement membrane; Cc = crystalline cone; Cg = corneagenous cell; Cr = cornea; R8 = distal retinula cell; Rc = retinula cell; Rd = rhabdom; Rp = reflecting pigment cell; Sp = screening pigment cell. (A) longitudinal section; (B, C) cross sections at the level of two adjacent bands in the distal layers of the rhabdom; (D, E) cross sections at two adjacent bands in the proximal rhabdom layers. (F) longitudinal section; (G) cross section at distal rhabdom layers.

data of the constituent parts of one representative central ommatidium of the compound eye of the two crustaceans are given in Table 1. From Figure 2 and Table 1 it is evident that the ommatidium of the deep-sea half-crab is much larger than that of the shallow-water species, even if differences in body size are taken into consideration.

#### *Dioptric apparatus*

A single facet of the eye of *Paralomis* is about 3 times larger in diameter and has a corneal lens that is 1.8 times thicker than that of a comparable shallow-water *Petrolisthes*. No significant difference between the two types could be detected, however, in the 200 μm thick periodic layers, revealed in longitudinal sections of the cornea along the optic axis. Two corneagenous cells, not noticeably different from those of *Petrolisthes* or any other decapod crustacean, occupied the space between cornea and cone.

The crystalline cone of *Paralomis* tapered only very gently and retained a much wider proximal diameter (Fig. 3a) than that of *Petrolisthes*. Whereas in *Petrolisthes*, cross sections through distal and central regions of the cone displayed square profiles and a content of electron-dense material, sections through the cone of *Paralomis* at corresponding levels exhibited rather circular outlines and a content of much looser consistency (Fig. 3b). When related to overall ommatidial length, the dioptric apparatus in the eye of *Paralomis* (though greatly enlarged in diameter) occupied significantly less space than the equivalent structure in the eye of the shallow-water *Petrolisthes*.

#### *Retinula and rhabdom*

In the eyes of other anomuran species—for example, *Petrolisthes* spp. (Eguchi *et al.*, 1982; Meyer-Rochow *et al.*, 1990) and *Munida* spp. (Bursey, 1975; Gaten, 1994)—a distal retinula cell (R8) with four cytoplasmic lobes occupies the tier between the crystalline cone and the seven regular retinular cells, but in *Paralomis* an ommatidial retinula is composed of only seven regular cells (1–7) and lacks the distal eighth cell. The distal end of the rhabdom is thus made up of seven regular retinula cells, which are in contact with the proximal end of the crystalline cone. It is in this region that the mottled retinula cell nuclei, with a maximum diameter of 7.5 μm, can be found.

The rhabdoms in *Paralomis* are extraordinarily well developed and occupy up to 85% of the available cytoplasmic space in the distal and central regions of the retinula (Fig. 4). The estimated membrane surface of an ommatidial rhabdom of *Paralomis* ( $231 \times 10^4$ ), calcu-

Table I

Comparison of biometrical data (in  $\mu\text{m}$ ) of ommatidia in the shallow-water *Petrolisthes* sp. and the deep-sea *Paralomis multispina*

	<i>Petrolisthes</i>	<i>Paralomis</i>	Para/Petro	Remarks
Cornea				
diameter	21	60	2.9	
thickness	16	28	1.8	
Crystalline cone				
distal diameter	20	56	2.8	length of a square side
prox. diameter	4	40	10.0	
length	110	110	1.0	
Ommatidial retinula				
length	60	390	2.6	
diameter	20	40	2.0	
Rhabdom				
diameter at nuclear layer	3.5	25	7.1	
diameter at proximal layer	$3 \times 8^*$	18	3.7	*rectangular
length	50	210	1.9	
thickness of one band	7	4–7	0.6–1.0	
diameter of one microvillus	0.08	0.11	1.4	
area of rhabdom membrane	$8.5 \times 10^4$	$231 \times 10^4$	27.2	total surface of microvilli/ommatidium
Rhabdom occupation ratio (%)				
distal and central region	12	85	6.3	
proximal region	35	45	1.3	
Distance from rhabdom end to BM	12	180	15.0	
Interommatidial angle	$4-6^\circ$	$3-5^\circ$	ca. 0.9	
Sensitivity	0.23	34.7	151	relat. sensitivities (after Land, 1981)

lated from the data in Table I, is about 27 times larger than that of *Petrolisthes* ( $8.5 \times 10^4$ ). Another comparison could be made with *Limulus*, which—even though it is not a crustacean—has a compound eye (Fahrenbach, 1969) superficially similar to that of *Paralomis*, but with

rhabdom occupation ratios generally lower than 10%. On the other hand, the hydrothermal vent shrimp *Rimicaris exoculata* occurs in a habitat similar to that of *Paralomis*, but its eye is highly aberrant, with volume densities of rhabdoms reaching 70%–80% (O'Neill *et al.*,

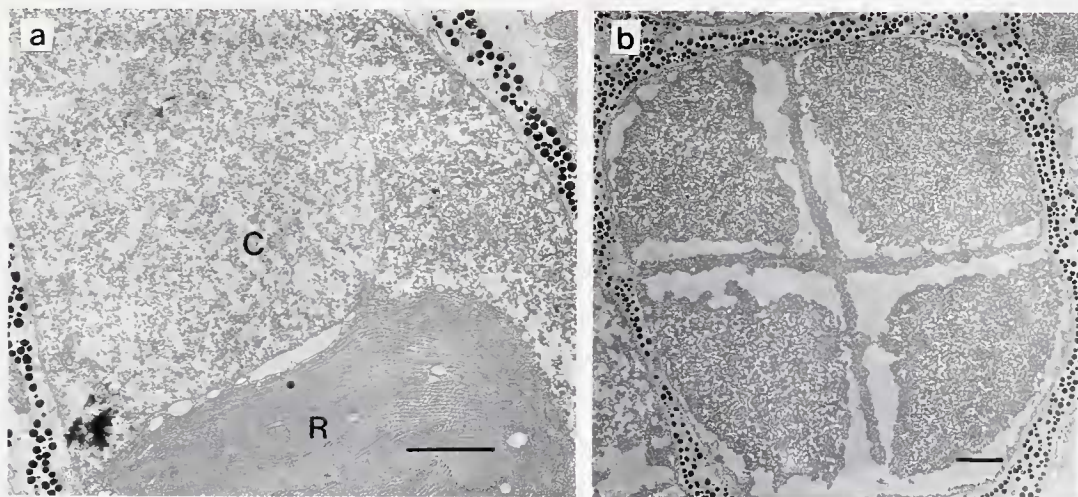
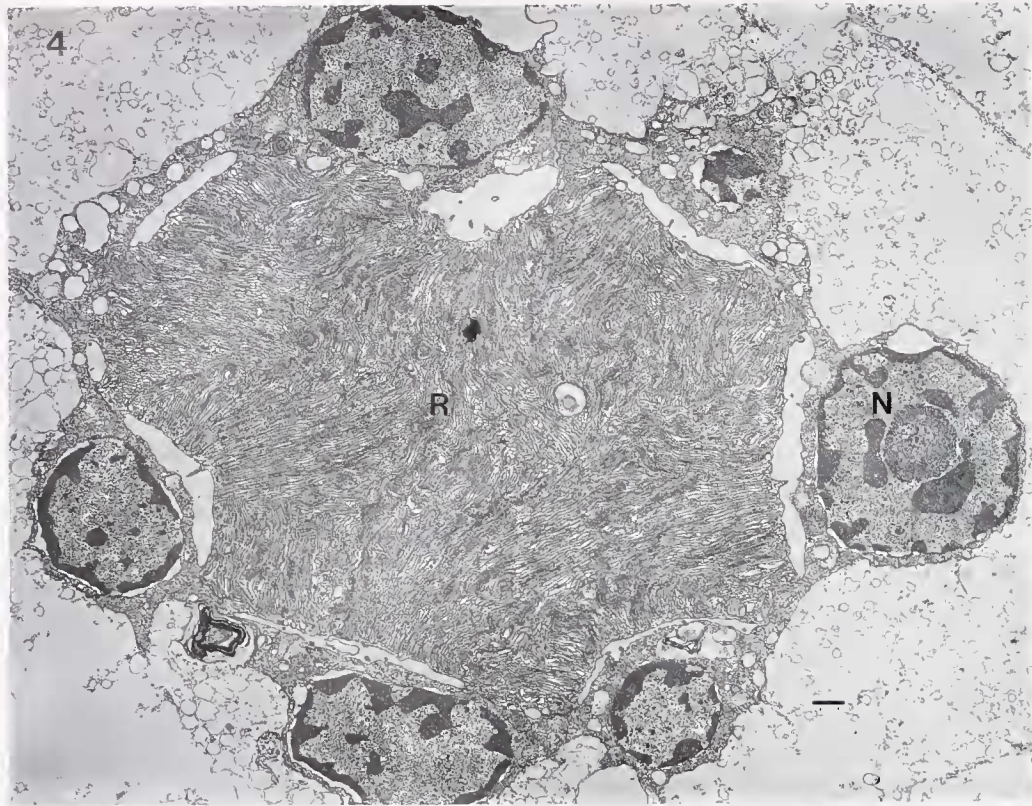


Figure 3. The deep-sea half-crab *Paralomis multispina*. (a) Longitudinal section through the proximal region of the crystalline cone and the distal tip. C = crystalline cone; R = rhabdom. Scale bar =  $5 \mu\text{m}$ . (b) Cross section through proximal part of crystalline cone with its four components. Numerous screening pigment granules surround the crystalline cone. Scale bar =  $5 \mu\text{m}$ .



**Figure 4.** Cross section of rhabdom at the retinula cell nuclear layer. Almost the entire cytoplasmic space of the retinula cells is occupied by the rhabdomeres. N = nucleus of retinula cell; R = rhabdom. Scale bar = 1  $\mu\text{m}$ .

1995). The retinula cells do not form proper rhabdoms in the proximal region; instead they gradually turn into slender axonal processes (Fig. 5).

Longitudinal sections reveal that the regular "bands," so typical for the rhabdoms of other decapods (including those of the shallow-water anomuran species), are almost lost in *Paralomis* and are replaced by microvilli running in many directions. This gives the rhabdom a somewhat irregular, disorderly appearance. Individual microvilli in *Paralomis* (Fig. 6) were thicker ( $0.11 \mu\text{m}$ ) than those of fully grown shallow-water *Petrolisthes* ( $0.08 \mu\text{m}$ ; Eguchi *et al.*, 1982; Meyer-Rochow and Reid, 1996). This difference has to be interpreted with caution, since it is known from other crustacean eyes (e.g., *Orchomene* sp.: Meyer-Rochow, 1981; *Mysis relicta*: Lindström *et al.*, 1988) that rhabdom microvilli have a tendency to swell and increase in diameter when suddenly exposed to very bright light.

The core-filament, usually identifiable in the lumen of a rhabdom microvillus of the crustacean eye, was missing or fragmented into smaller pieces (Fig. 7). Some of the rhabdom microvilli exhibited flattened or swollen structures in the place where core-filaments with their associated side-arms should have been. Since core-

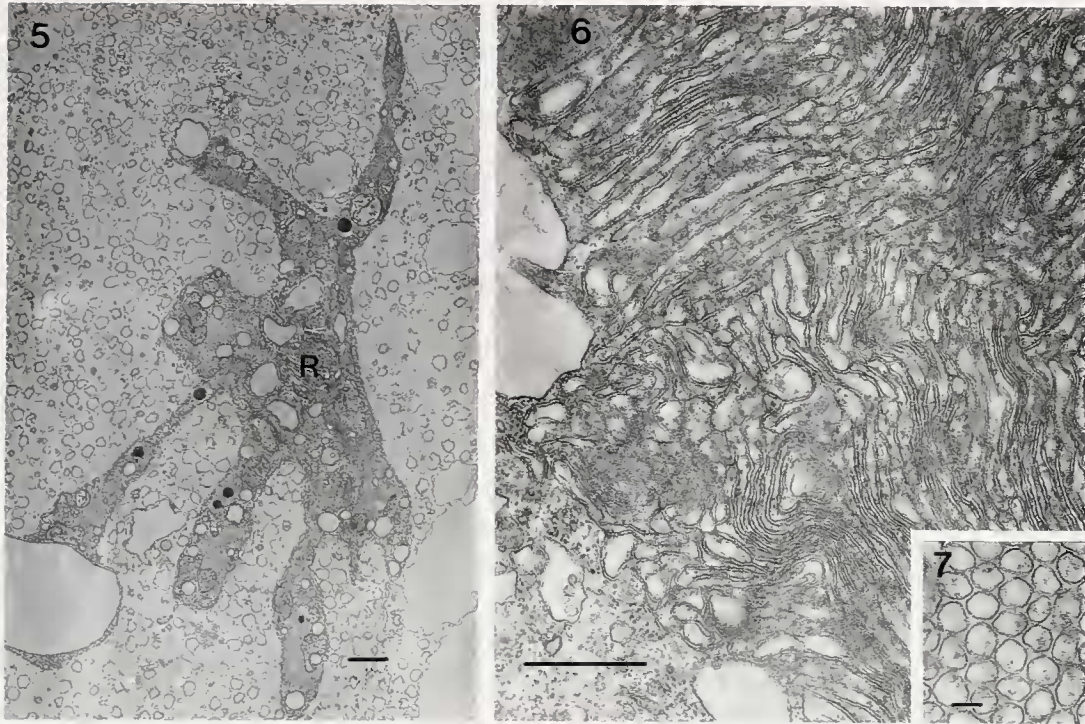
filaments and their associated side-arms in compound eyes are fragile and easily destroyed by irradiation with bright light (Blest *et al.*, 1982; Tsukita *et al.*, 1988), their disruption in our material could stem from the brief exposure to sunlight during capture.

#### Screening pigment

The eye of *Paralomis* lacks secondary pigment cells; two primary pigment cells are found around the crystalline cones and contain spherical electron-opaque pigment grains of about  $0.4 \mu\text{m}$  in diameter (Fig. 3a). The density of these granules seems not to differ from that of granules in the shallow-water half-crabs, but screening pigment granules in the retinula cells are far less numerous in *Paralomis*. In place of secondary pigment cells are an unknown number of cells presumed to contain reflecting granules.

#### Reflecting pigment

The distance between the proximal end of the rhabdom and the basement membrane of an ommatidium is relatively short in *Petrolisthes* and other shallow-water



**Figure 5.** Cross section through proximal retinal layer. A small rhabdom (R) is seen at the center of a cluster of seven retinula cells. A few scattered screening pigment granules are visible in some of the retinula cells. Well-developed reflecting pigment cells fill the interommatidial spaces. Scale bar = 1  $\mu\text{m}$ .

**Figure 6.** Cross section through a segment of a retinula cell demonstrating the multidirectional orientation of microvilli in the rhabdom. Scale bar = 1  $\mu\text{m}$ .

**Figure 7.** Higher magnification of transversely cut microvilli of the rhabdom. Note that core-filaments are lost in some of the microvilli. Scale bar = 0.1  $\mu\text{m}$ .

decapods. In *Paralomis*, however, this same distance is strikingly long (ca. 180  $\mu\text{m}$ ). In the proximal layer, the retinula cells become slender as shown in Figure 5. The space thus made available is filled with enormously developed cells containing large amounts of reflecting pigments. The extensions of the reflecting pigment cells, which are easily identifiable by their innumerable 0.3- $\mu\text{m}$ -wide vesicles, penetrate between the retinula cells of individual ommatidial units, thus apparently increasing their effectiveness in reflecting light towards the more distally placed rhabdom.

### Discussion

Eguchi *et al.* (1982) suggested that anomuran half-crabs of the superfamily Galatheoidea possess reflecting superposition eyes. Research by Meyer-Rochow *et al.* (1990) on the galatheid *Petrolisthes elongatus* and by Gaten (1994) on *Munida rugosa* lent further support to this notion, but specified that this was true only for the dark-adapted eye; in the light-adapted state apposition optics

were used. It is generally assumed that superposition eyes are more useful than apposition eyes in dim light, for the former are typical of many nocturnal crustaceans and deep-sea forms.

It is, therefore, a little surprising to find that the eye of the deep-sea anomuran galatheid *Paralomis multispina* (a) lacks a wide clear-zone, which is normally considered a prerequisite for any form of superposition vision (Land, 1981), and (b) possesses roundish rather than regular, square cones, which are an essential requirement for reflecting superposition (Land, 1976; Vogt, 1980). The species does, however, exhibit other kinds of modifications that are more in keeping with adaptations to an extremely dim environment: compared with the shallow-water half-crabs of the genus *Petrolisthes* (Eguchi *et al.*, 1982; Meyer-Rochow *et al.*, 1990), in *Paralomis* the corneal diameter is three times greater, and cone as well as rhabdom diameters are even more enlarged (Table I). The reflecting tapetum on the proximal side of the retinula is massively developed, and it is evident that the eye is designed to maximize photon capture. The fine-struct-

tural disruptions and larger diameters of the rhabdom microvilli seen in *Paralomis* are almost identical to those reported from the eyes of deep-water amphipods from the Antarctic (Meyer-Rochow, 1981) and are most likely caused by the exposure to bright light during capture. Indirectly the disruptions thus point to a high absolute sensitivity to light, but at the same time they obscure signs for or against membrane shedding (cf. Chamberlain and Barlow, 1984).

On the basis of the definition that Land (1981) provided for "absolute sensitivity," we calculated sensitivities of light-adapted eyes of *Paralomis* and those of shallow-water *Petrolisthes*: the eye of *Paralomis* was 150 times more sensitive. The comparison is based on the assumptions that the extinction coefficient ( $k$ ) is the same for the two species and that the types and densities of pigments found in the rhabdoms are identical (cf. discussion in Ziedins and Meyer-Rochow, 1990). If one assumes a superior photopigment content in the dark-adapted *Paralomis* eye and considers thermal noise reduction at low environmental temperatures (Aho *et al.*, 1988), the overall sensitivity advantage of *Paralomis* over *Petrolisthes* to extended light sources may be even higher.

If the lack of a clear-zone is real and not artifactual (clear-zones in the superposition eyes of deep-sea decapods can easily collapse and, on account of their fragility and delicateness, may remain undetected as shown by Nilsson, 1990), the closer approximation of the massively developed rhabdom to the much wider dioptric elements, in combination with the backing of a tapetum from behind, could be interpreted as an adaptation to improve sensitivity, especially to point sources. The shortening of both cornea and cone, relative to the overall length of one ommatidium, and the loss of the orderly arrangement of microvilli in the rhabdom also point toward an adaptation to minimize photon loss and maximize photon capture (Laughlin *et al.*, 1975). The considerably greater rhabdom-occupation ratio in the eye of *Paralomis* as compared with the shallow-water species not only allows more photopigment molecules to be packed into the visual membranes, but also indicates low energy demand and slow cellular metabolism, both adaptations that are extremely useful in the deep-sea environment (Elofsson and Hallberg, 1977).

In the shallow-water *Petrolisthes elongatus* the eye enlarges as the half-crab grows; ommatidia are added and sensitivity to both extended and point sources increases. *P. elongatus* uses vision to detect and approach hiding places (Meyer-Rochow and Meha, 1994). Since signs of eye regression in adult *Paralomis* are missing, we must assume that the general growth pattern resembles that of *Petrolisthes*. This, however, raises the question of what

*Paralomis* could possibly see at a depth of 1200 m, the "limit" beyond which sunlight can no longer be detected (Clarke and Kelly, 1964). Biological light sources, however, abound at this depth (Omori, 1974), and it may well be in the interest of a benthic, sedentary detritus and filter feeder to notice them. Any visual signal adult *Paralomis* could possibly be interested in would almost never come from below, and this could explain the lack of regional eye specializations seen in so many mesopelagic shrimps (Gaten *et al.*, 1992).

We know nothing about the spectral sensitivity of *Paralomis*, but the visual pigments of eight other anomuran species all exhibit a single absorption peak in the bluegreen region of the spectrum (Cronin and Forward, 1988). Ziedins and Meyer-Rochow (1990) electrophysiologically measured spectral sensitivity peaks of dark- and light-adapted eyes of *P. elongatus* and also found them to lie in the bluegreen part of the spectrum. Since even the eyes of the hydrothermal vent species *Rimicaris exoculata*, which are strongly modified morphologically (O'Neill *et al.*, 1995), possess a sensitivity peak in the bluegreen (Johnson *et al.*, 1995), we do not expect the eyes of *Paralomis* to differ in this respect. However, the lack of secondary screening pigments and retinula cell 8 in *Paralomis* suggests that the eye of *M. rugosa*, for example, is less well adapted to the greatest depth of its range (shallow water down to 1250 m: Gaten, 1994) than that of *Paralomis*. *M. rugosa* appears to be a relative "newcomer" to the deep-sea, while *Paralomis* has been exploiting that habitat for a longer evolutionary period. How much longer is hard to say, but Nuckley *et al.* (1996) speculate that a hydrothermal vent shrimp with modified eyes may have "migrated from the surface possibly in the last 5,000–10,000 years" and over that period evolved its present eye morphology.

In conclusion, the hypertrophied rhabdoms in the eye of *Paralomis*, the loss of the orderly microvillus arrangement, the reduction of the cytoplasmic component of the retinula cells, the massively developed layer of reflecting vesicles in the proximal half of the retinula, and (considering overall ommatidial length) the relative shortening of the dioptric elements coincident with greatly enlarged diameters in the eye of *Paralomis* are all consistent with depth-related adaptations seen also in the eyes of deep-sea mysids (Elofsson and Hallberg, 1977), amphipods (Hallberg *et al.*, 1980; Meyer-Rochow *et al.*, 1991), and to some extent other benthic decapods (Hiller-Adams and Case, 1985) and mesopelagic shrimps (Gaten *et al.*, 1992). However, the eyes of deep-water euphausiids (Hiller-Adams and Case, 1988) are least similar to those of *Paralomis* and this, we believe, has to do with (a) the widespread ability of euphausiids to produce light, (b) the greater mobility and pelagic lifestyles of euphausiids,

and (c) the longer evolutionary period euphausiids have had to adapt their photoreceptors to the deep-sea environment.

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